ENERGY COST OF STANDING IN ADULT MOOSE

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Abstract: The energy cost of standing in adult moose (Alces alces) was 0.23 kcal/hr/kg or 1.0 kcal/hr/kg.75, an increase of 22% over the cost of lying during the winter season. Moose had a lower cost of standing than many other wild ruminants.

Energy costs of various activities, in combination with daily activity budgets, are used to calculate daily energy expenditure of free-ranging animals. Values for daily energy expenditure are used in simulation models to predict nutritional carrying capacity of ranges (Hobbs et al. 1982, Swift 1983) or the influence of disturbance on energy expenditure (Fancy 1986). The cost of standing in wild ungulates is often crudely estimated as an additional 9% of the lying costs based on early work with sheep and cattle (Brody 1945). Recent studies with wild ungulates have indicated that a 9% increment for standing is low, and great variability exists among species (Robbins 1983).
Most authors have followed the convention developed for domestic livestock and expressed the cost of standing as a percentage of the resting metabolic rate. In wild ruminants the resting metabolic rate varies greatly by season, but the cost of standing is unlikely to be affected by seasonal fluctuations. Therefore, values for incremental costs of activities in wild ungulates are best expressed as a rate (kcal/hr/kg or kcal/hr/kg\(^{0.75}\)) rather than as a percentage of resting metabolic rate. This paper reports on the incremental cost of standing in adult moose (*Alces alces*) and compares these data with other ungulate species.

**METHODS**

An indirect respiration chamber was used to measure the heat production (HP) of adult moose at the Moose Research Center near Soldotna, Alaska (Regelin et al. 1981). The moose were captured at birth, hand-reared, and trained (Regelin et al. 1979) for use in a respiration chamber. Heat production in both a fed and fasted state was measured throughout the year on three male and three female moose that ranged in age from 2 to 5 years (Regelin et al. 1985). Position of the moose was monitored continuously during each 12-hour metabolic trial; measurements of HP were made whenever a moose had remained in a standing or lying position continuously for 2 hours. The cost of standing was calculated to be the difference in HP between consecutive 2-hour periods of lying and standing. Moose activity during
standing periods was subjectively rated as calm, active, or very active.

RESULTS AND DISCUSSION

There were 65 opportunities throughout the year to calculate the cost of standing; however, the moose stood calmly with minimal movement for the entire 2-hour period in only 13 cases, all during the winter period. The cost of standing over lying in these calm animals averaged $0.23 \pm 0.011 \text{ kcal/hr/kg}$ or $1.01 \pm 0.071 \text{ kcal/hr/kg}$ $^{75}$ ($\bar{x} \pm 95\%$ confidence interval) with a range of 0.12 to 0.28 kcal/hr/kg. These winter measurements represented a 22% increase over the metabolic rate of lying animals (range 12-28%). Six values were from fed animals and seven from animals fasted for 48 hours. No differences were noted between values from fed or fasted animals. All 65 values were examined to determine if the cost of standing varied by season. No significant differences ($P < 0.05$) between seasons were observed, but data were variable due to differences in movement associated with standing. The 65 values measured ranged from 0.122 to 1.28 kcal/hr/kg, or 12 to 148% above the cost of lying. The high values were measured with moose that were moving more than 50% of the time. No significant differences in cost of standing were noted due to sex of the moose.

Values measured in this study are slightly higher than those reported from moose in Alberta by Renecker and Hudson
(1983). They used a calibrated heart rate index to estimate the cost of standing at 0.19 compared with 0.23 kcal/hr/kg in this study. The higher value measured in this study is likely due, at least in part, to movement during the 2-hour measurement period. Even though Renecker and Hudson (1983) reported a lower rate, their percentage increase of standing over lying was higher than ours by 7% (29% vs. 22%), demonstrating the problem of expressing the cost of standing as a percentage of resting metabolic rate. A later study by Renecker and Hudson (1986) measured the cost of standing by indirect calorimetry. The incremental cost of standing in this study was 1.0 kcal/hr/kg^0.75, exactly the same as this study.

A comparison of the cost of standing for different species reveals a wide range of values (Table 1). Many authors did not provide individual body weights of the animals they measured; where possible we calculated an estimated weight to provide comparable units of measure. Domestic cattle and sheep had the lowest values, perhaps due to less anxiety or alert behavior than wild animals. In general, large animals (moose and elk [Cervus elaphus]) had a smaller energy requirement for standing than smaller animals, but bighorn sheep (Ovis canadensis) were a notable exception. The values for white-tailed (Odocoileus virginianus) and mule deer (Odocoileus hemionus) are likely too high due to problems with movements while standing.
Table 1. Energetic cost of standing in several ruminant species.

<table>
<thead>
<tr>
<th>Species</th>
<th>%</th>
<th>kcal/hr/ kg</th>
<th>kcal/hr/ kg&lt;sup&gt;75&lt;/sup&gt;</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Roe deer</td>
<td>22</td>
<td>0.52&lt;sup&gt;a&lt;/sup&gt;</td>
<td>1.1</td>
<td>Weiner 1977</td>
</tr>
<tr>
<td>Antelope</td>
<td>21</td>
<td>0.80</td>
<td>1.9</td>
<td>Wesley et al. 1973</td>
</tr>
<tr>
<td>Bighorn sheep</td>
<td>18</td>
<td>0.18</td>
<td>0.5</td>
<td>Chappel &amp; Hudson 1979</td>
</tr>
<tr>
<td>White-tailed deer&lt;sup&gt;b&lt;/sup&gt;</td>
<td>63</td>
<td>0.92</td>
<td>2.4</td>
<td>Mautz &amp; Fair 1980</td>
</tr>
<tr>
<td>Mule deer</td>
<td>72</td>
<td>--</td>
<td>--</td>
<td>Kautz et al. 1982</td>
</tr>
<tr>
<td>Elk</td>
<td>30</td>
<td>0.45&lt;sup&gt;c&lt;/sup&gt;</td>
<td>1.5</td>
<td>Gates &amp; Hudson 1979</td>
</tr>
<tr>
<td>Elk calves</td>
<td>25</td>
<td>0.44&lt;sup&gt;d&lt;/sup&gt;</td>
<td>1.2</td>
<td>Parker et al. 1984</td>
</tr>
<tr>
<td>Moose</td>
<td>22</td>
<td>0.23</td>
<td>1.0</td>
<td>This study</td>
</tr>
<tr>
<td>Moose</td>
<td>29</td>
<td>0.19&lt;sup&gt;e&lt;/sup&gt;</td>
<td>0.8</td>
<td>Renecker &amp; Hudson 1983</td>
</tr>
<tr>
<td>Moose</td>
<td>25</td>
<td>0.23&lt;sup&gt;e&lt;/sup&gt;</td>
<td>1.0</td>
<td>Renecker &amp; Hudson 1986</td>
</tr>
<tr>
<td>Moose calves</td>
<td>35</td>
<td>0.65</td>
<td>1.9&lt;sup&gt;f&lt;/sup&gt;</td>
<td>Renecker et al. 1978</td>
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<tr>
<td>Reindeer</td>
<td>10</td>
<td>--</td>
<td>--</td>
<td>White &amp; Yousef 1978</td>
</tr>
<tr>
<td>Domestic cattle</td>
<td>19</td>
<td>0.14</td>
<td>0.57&lt;sup&gt;g&lt;/sup&gt;</td>
<td>Vercoe 1973</td>
</tr>
<tr>
<td>Domestic sheep</td>
<td>13</td>
<td>0.12</td>
<td>--</td>
<td>Webster &amp; Valks 1966</td>
</tr>
</tbody>
</table>

<sup>a</sup> Estimated weight of 20 kg.
<sup>b</sup> Standing included movement up to 50% of time.
<sup>c</sup> Estimated weight of 125 kg.
<sup>d</sup> Estimated weight of 50 kg.
<sup>e</sup> Estimated weight of 325 kg.
<sup>f</sup> Estimated weight of 85 kg.
<sup>g</sup> Estimated weight of 273 kg.
Differences among species in the energy cost of standing may be due in part to morphological differences and should be examined from this viewpoint. Different costs for standing and locomotion likely lead to differences in feeding strategies and other behavior and play a role in habitat selection and niche separation of wild ungulates.

REFERENCES


